

A COMPARISON OF THE NEST PHENOLOGIES OF
THREE SPECIES OF *POGONOMYRMEX* HARVESTER
ANTS (HYMENOPTERA: FORMICIDAE)*

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INTRODUCTION

Ants are among the most abundant animals in most habitats (Petal 1967) and may even be the dominant insects in many ecosystems (Nielsen 1972; Nielsen and Jensen 1975). Harvester ants of the genus *Pogonomyrmex* are a major component of the energy flux through ecosystems (Golley and Gentry 1964). Ants of this genus have become increasingly important in ecological studies, including mutualism (O'Dowd and Hay 1980), competition (Mares and Rosenzweig 1978; Reichman 1979; Davidson 1980), predation (Whitford and Bryant 1979), foraging (Whitford and Ettershank 1975; Hölldobler 1976a; Whitford 1976, 1978a; Davidson 1977a, b; Taylor 1977), community structure (Davidson 1977a, b; Whitford 1978b), and impact on ecosystems (Clark and Comanor 1975; Reichman 1979). It is difficult to investigate harvester ants as seasonal processes occurring inside the nest are generally unknown and the nest populations are usually underestimated.

This investigation compares the nest phenologies of three species of *Pogonomyrmex* harvester ants: *P. montanus* MacKay, *P. subnitidus* Emery, and *P. rugosus* Emery, which occur at high, mid, and low altitudes respectively. These data form the basis for a comparison of the ecological energetics of the three species (MacKay 1981).

MATERIALS AND METHODS

The species investigated.

The altitudinal comparison is based on three species of harvester

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ants: *Pogonomyrmex montanus* MacKay, *P. subnitidus* Emery, and *P. rugosus* Emery. All three belong to the subgenus *Pogonomyrmex*. *Pogonomyrmex subnitidus* and *P. montanus* are very closely related, both belong to the *occidentalis* complex (MacKay 1980). *Pogonomyrmex rugosus* belongs to the *barbatus* complex (Cole 1968). *Pogonomyrmex montanus* is unusual for the genus in being a high mountain species occurring in pine forests in the mountains of southern California. *Pogonomyrmex subnitidus* is a mid-altitude species in the San Jacinto Mountains. *Pogonomyrmex subnitidus* is distributed throughout southern and south central California and Baja California, occurring at lower elevations throughout much of its range. *Pogonomyrmex subnitidus* is sympatric with *P. rugosus* in parts of Riverside County, but is uncommon in such areas. *Pogonomyrmex rugosus* is a low altitude species near Riverside and occurs at lower elevations throughout much of southwestern United States. It rarely occurs at higher elevations. For example, in the Joshua Tree National Monument it is present up to 1350 meters, in New Mexico it occurs at over 2100 meters.

Study areas.

Populations of all three species were studied in southern California: *P. montanus*—in a yellow pine forest community between Fawnskin and Big Pine Flat at 2100 meters elevation in the San Bernardino Mountains of San Bernardino Co., *P. subnitidus*—in the chaparral near the Vista Grande Ranger Station at 1500 meters in the San Jacinto Mountains of Riverside Co., *P. rugosus*—in the coastal sage scrub community at Box Springs at 300 meters near Riverside, Riverside Co. The three species occur in clearings within these different plant communities.

Estimation of nest populations.

Two primary methods are used in the estimation of ant nest populations: mark-recapture methods and nest excavation. Mark-recapture methods are used to compare a population before and after seasonal production. This method has been criticized as one of the assumptions is that workers mix randomly in the nest. The workers of all three species are stratified within the nests and there is strong evidence that other species are stratified as well (MacKay 1981). Also I could find no reliable way to mark the individuals such that the marks were permanent, could not be passed on to other individuals, and would not disrupt normal activities. In any case,

such a method would only estimate the numbers of foragers in a *Pogonomyrmex* nest, not the actual nest population. In addition, mark-recapture methods do not provide an estimate of the reproductives produced in a nest.

Excavation of nests destroys them for further study and requires a large expenditure of time and effort. I chose periodic nest excavation as the method of estimating production as counts of the sexuals, brood, and workers can be made.

Our experience indicates that most of the nest population is collected. *Pogonomyrmex* spp. colonies may live 15 to 20 years (Barnes and Nearney 1953), and will live at least two years after the removal of the queen (pers. obs.). Nest longevity is unknown in the three species investigated, but based on data from other species, I expect at least 5%–10% of the nests should not have queens. The high proportion of nest queens collected (84% in *P. montanus*, 77% in *P. subnitidus*, and 80% in *P. rugosus*) supports the hypothesis that most of the nest population is collected. The queens do not reside in any special “queen chamber” and are of a similar size as a worker. Therefore, it is not any easier to find the queen than it is to find any individual worker in the nest. In all cases excavation was continued at least 50 cm deeper than the position of the last ant found or the end of a burrow.

Nest excavation procedure.

The procedure was as follows: The surface dimensions of the nest were determined by removal of the top 10 cm of the nest. The hole was then extended at least 50 cm on all sides. A square ditch was dug around the perimeter of the nest to a depth of one meter in the case of *P. montanus* nests and over 1.5 meters around the nests of *P. rugosus* and *P. subnitidus*. We were able to sit in the ditches while carefully excavating the nests in 10 cm levels. As the hole became deeper, the ditches were proportionally deepened. All of the contents of the burrows, including ants, brood, guests, stored seeds, and dirt were placed in labeled half or one liter plastic containers. Later the animals were separated from the dirt, and counted. Nest excavation usually began between 06:00 and 07:00, before the ants became active. If foragers were needed for other investigations, excavation began later in the morning or early in the afternoon. Excavation and counting of a *P. montanus* nest requires 6–10 hours, of a *P. subnitidus* nest 20–30 hours and of a *P. rugosus* nest 60–90

hours. Whenever excavation was stopped to be continued on the following day, the nest was covered with a heavy vinyl cloth and 10 cm deep layer of dirt. This was necessary to keep the inhabitants, especially the males, in the nest. A total of 80 *P. montanus*, 26 *P. subnitidus*, and 20 *P. rugosus* nests were completely excavated between 1977 and 1980.

It appeared that the excavation procedure disrupted stratification of individuals within the nest only slightly. When nest chambers were exposed, many individuals emerged, but most of the population remained in the chambers, and assumed a defensive position involving opening of the mandibles and forward extension of the antennae.

The numbers of workers at each level and the position of the queen were recorded. When the nests were in production, the presence or absence of eggs was noted, but the eggs were not counted, as they were extremely small and are easily lost in the dirt. The larvae, pupae, females, males, and callows (immature, underpigmented workers) were counted when they were present in the nests. The contents of each level were summed to obtain an estimate of the entire nest population.

Seed storage in nests.

The seeds were separated from the soil by filling a 1000 ml beaker about $\frac{3}{4}$ full of soil and seeds. The contents were washed into a sieve with 0.5 mm mesh. The washing and swirling were continued until all of the seeds were removed from the soil. The material caught in the sieve was washed again until only seeds remained in the sieve. The seeds were then dried (60° C) to constant weight.

Nest structure.

In the process of nest excavation it was noted that the general form and shape of the nests were comparable in all three species. The *P. montanus* nest structure was studied by pouring a thin solution of plaster of Paris (3 tablespoons/liter of water) into one nest. The solution was dilute enough that the walls of most of the tunnel system were coated with plaster. The nest was excavated in 1-2 cm layers and the tunnel structure at each layer was measured and sketched. The resulting series of "cross sections" of the nest resulted in a composite drawing of the nest.

Nest temperature and humidity.

Temperature data were recorded from approximately weekly

readings of thermistors permanently implanted in nests of the three species. The data were supplemented with readings taken during nest excavation, following the procedure of Rogers et al. (1972). Soil temperatures taken within the excavation hole (at least 20 cm distant from ant burrows) and within the adjacent undisturbed soil at the same level were not significantly different in two cases involving *P. montanus* nests ($F = 0.00001ns$, $F = 0.13ns$). Similar comparisons were not made in the cases of *P. rugosus* and *P. subnitidus* as the soils were too compacted to allow the insertion of a thermometer in undisturbed soil to a depth of 30 or 40 cm.

Soil samples (160 grams) were collected at various depths and oven dried ($60^{\circ}C$) to constant weight to determine water content. At least three replicates of soil temperature and soil moisture content were collected at each level. It was anticipated that these parameters would determine the position of the brood within the nest. I assumed a correlation existed between the humidity within the burrows and water content of the soil as well as a uniformity of the soil structure in the first 100 cm of the nest where most of the seasonal changes in the positions of the inhabitants occurred. Sandy soils would release more water vapor to burrows than would clay soils, if both had the same level of soil moisture (Marshall and Holmes 1979). The amount of water present within the soil changes continuously under field conditions (Marshall 1959), which would also modify the relative humidity.

Food input into nest.

Food input was estimated by channeling the flow of foragers and sampling a fraction of foragers at regular intervals to determine the numbers of trips made and the amount of food brought back to the nest.

Twenty-eight nests of the three harvester ant species (13 *P. montanus*, 10 *P. subnitidus*, and 5 *P. rugosus*), were surrounded by strips of 25 gauge sheet metal. The diameters of the enclosures were approximately one meter for *P. montanus*, 1.5 meters for *P. subnitidus*, and 2 meters for *P. rugosus*. The sheet metal strips were buried to a depth such that 10 cm of the metal were exposed. Sheet metal with a total width of 20 cm was sufficient. The ants could not normally climb over the enclosure as the sheet metal was very smooth. The ants would occasionally begin to climb the enclosure at the junction of the two ends. In such cases the area was covered with Tanglefoot(R).

In some cases, especially with *P. montanus*, the ants would attempt to tunnel under the enclosure. When this occurred, the ants were removed from the site of the tunneling and placed near the nest entrance inside the enclosure. In such cases the tunneling was completely controlled by destroying the tunnel system and replacing it with soil.

The ants were allowed to enter and exit the colony through two 2 cm diameter vinyl tubes, 6 cm in length. Entrance of the ants to the colony through the "exit" tube was prevented by having a 0.5–1 cm distance between the end of the tube and the soil. In a similar manner exit via the "entrance" tube was prevented. The ants were apparently not affected by this short distance, they either simply dropped with no hesitation or rapidly climbed down from the tube to the soil. The tubes were within 15 cm of each other and were placed on the side of the nest where most of the foraging occurred. A 0.448 liter glass jar could be placed under the tube by which the ants entered the nest, thus collecting the foragers with the food items they carried. The foragers were counted and the food items collected. The foragers were released into the nest enclosure with a quantity of food (native seeds) which approximated the amount of food removed. The nests were sampled at approximately weekly intervals throughout the foraging seasons, during 1978 to 1980. All of the foragers entering *P. montanus* nests were collected, 1/5 to 1/6 of those entering *P. subnitidus* nests, and 1/60 of those entering the *P. rugosus* nests. With these proportions, one person could handle the activity of 5 nests during a single day. The forager populations were estimated by capturing all of the foragers throughout the day, as they returned to the nests.

Statistical analysis.

Unless otherwise indicated, the 5% level of significance was used in all comparisons. A single asterisk indicates statistical significance at the 5% level, double asterisks at the 1% level, triple asterisks indicate significance at the 0.1% level. Means are listed plus or minus one standard error. The percentages of the nest populations were used to make comparisons between the species possible. The data obtained were fit to least squares polynomial regressions (Snedecor and Cochran 1967). The curves were constructed from the equations.

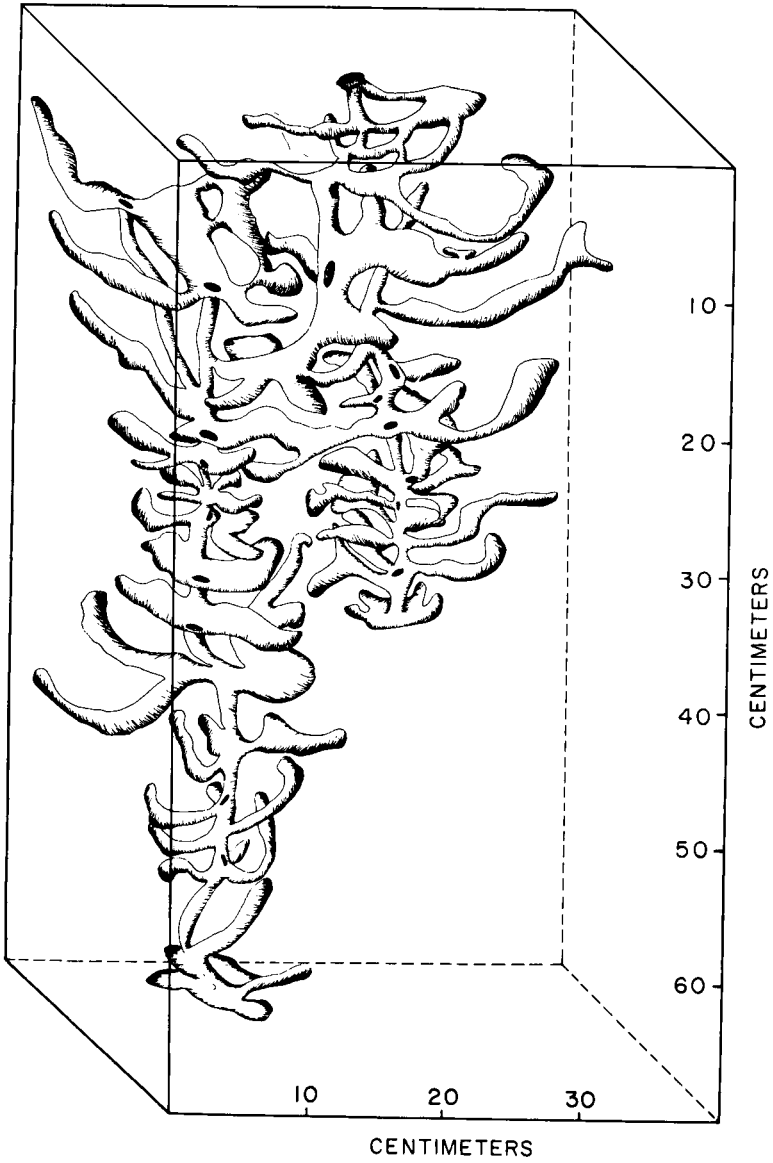


Figure 1. The structure of a typical *Pogonomyrmex montanus* nest.

RESULTS

Nest structure.

The nest of *P. montanus* has numerous burrows in the upper levels (Figure 1). Below this, there is often only a single main tunnel to the bottom of the nest. Most of the ants are found in the burrows which branch from the main tunnel. The main tunnel contains few ants and is apparently used only for movement between the side burrows. In many cases there are two separate "major tunnels", as is shown in Figure 1. In *P. subnitidus* the two major tunnels may be separated by more than 100 cm and may appear as two separate nests. One major tunnel may contain no brood and the other may contain all of the brood in the nest. The queen and brood are usually found in the major tunnel which goes to the deeper level.

The structure of the nests of *P. subnitidus* and *P. rugosus* are not shown, but are similar except that they are larger and deeper, often extending to 300 or 400 cm deep. There was no relationship between the worker populations and the nest depth (for *P. montanus* $r = 0.16ns$ (65), for *P. subnitidus* $r = 0.03ns$ (26), and for *P. rugosus* $r = 0.32ns$ (20)).

Nest microclimatology: temperature.

The seasonal changes in nest temperatures are similar for all three species (Figure 2). The nest warms rapidly in the spring and temperatures reach a maximum at the end of June or July. The soil temperature begins to drop in August and levels out during the winter months. As the species occur at different altitudes, the temperature ranges are different. The range of *P. montanus* extends from slightly below zero to 20° C, that of *P. subnitidus* from slightly above zero to 25° C, and that of *P. rugosus* from slightly below 10 to 30° C.

Only the changes at the 20 and 50 cm depths are shown in Figure 2 as the other levels are similar. The differences between the levels deeper than 40 cm were generally not significant. The only important difference between the curves of the 20 cm level and 50 cm level is that the shallow level warmed sooner in the spring and cooled sooner in the fall.

Nest microclimatology: humidities.

The seasonal changes in soil moisture are similar in the nests of all three species (Figure 3). Soil moistures are high in the winter and

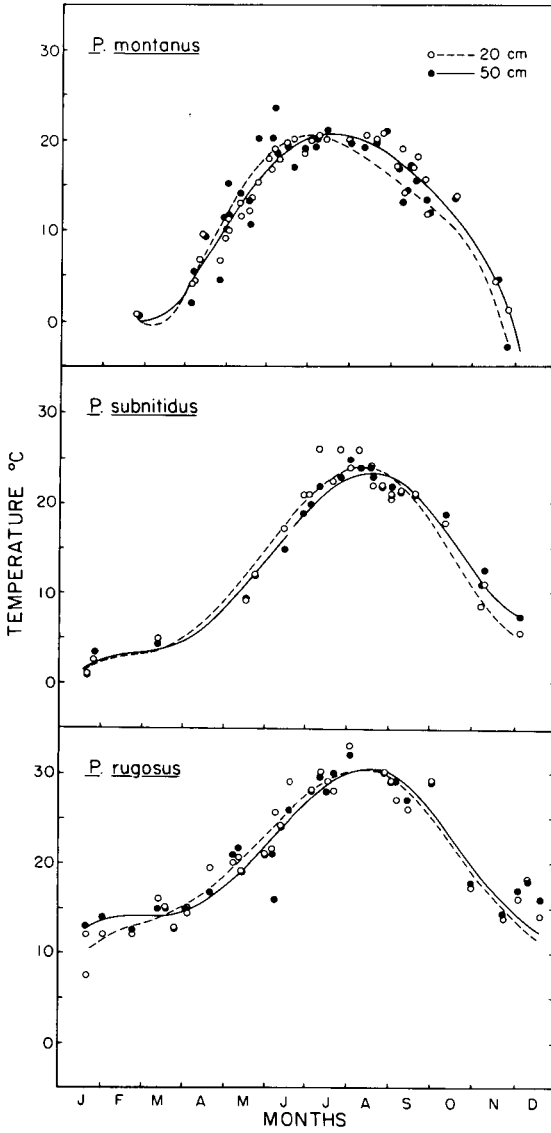


Figure 2. Seasonal changes in the mean daily nest temperatures of three species of *Pogonomyrmex* harvester ants.

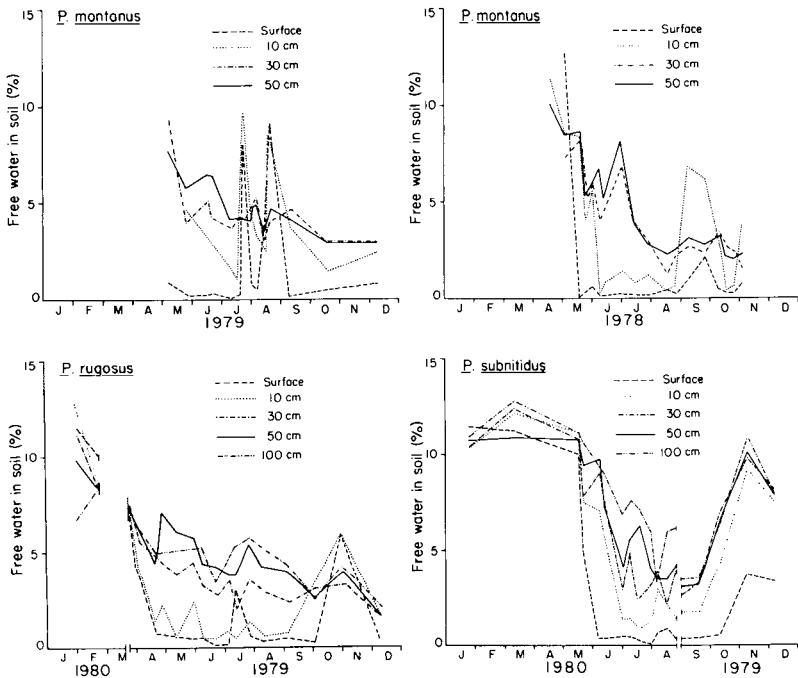


Figure 3. Seasonal changes in the nest humidities of three species of *Pogonomyrmex* harvester ants.

spring and low in the summer and fall. Throughout the winter, the soils receive relatively large amounts of rain or snow which raise the soil moistures to high levels. After this time, the surface and upper levels lose water rapidly by evaporation. The lower levels of the nest retain water throughout the entire season, although the percentage decreases. Soil moistures at levels below 30 cm are essentially the same for all three species. Summer showers rapidly increase soil moistures of the upper levels (note the peaks in the Figure 3), but have little effect on the levels below 30 cm. This water input into the soil is rapidly lost by evaporation.

The soil moisture of the lower levels is generally higher than that of the upper levels, possibly forming a relative humidity gradient. There are more fluctuations in the higher levels, both in soil

moisture and temperature. This probably accounts for much of the brood being kept in the lower nests levels.

The harvester ants apparently obtain water from several sources. Some metabolic water may be available to the ants, as it has been shown that harvester ants increase their metabolism when they are water stressed, without increasing their activity (Ettershank and Whitford 1973; Kay and Whitford 1975). Morning dew would not normally be available as foraging begins after dew has evaporated. I have seen harvester ants actively drink rain drops on the soil surface, demonstrating a curious pumping action of the gaster, but precipitation is not common in the three habitats during the summer (U.S. Weather Bureau Climatological Data). Capillary condensation occurs in the soil at relative humidities above eighty percent (Rode 1955) and may allow the ants free water. Arthropods, especially insects, are able to actively absorb water vapor from unsaturated air, although the mechanism is not understood (Edney 1974; Cloudsley-Thompson 1975). It is not known if harvester ants have the ability to actively absorb water vapor.

Seasonal changes in nest populations.

The data on nest populations obtained from the nest excavations are summarized in Appendix 1. Absolute counts could not be easily compared because the numbers of individuals present in the nests of the three species are very different. To reduce this variation between nest populations of the three species, the data are compared in the form of percentages. The seasonal changes in the brood and sexual populations are similar for all three species, when the percentage composition of each of the classes are compared (Figs. 4 & 5). In the three species, egg laying begins in late April to late May, similar to *P. owyheeii* (Willard and Crowell 1965) and *P. occidentalis* (Lavigne 1969). Development from egg to callow in the species requires five to six weeks compared to 25 days for *P. badius* (Gentry 1974) and 30 days in *P. occidentalis* (Cole 1934). It is very difficult to determine the number of larval instars in the development of ants (Wheeler and Wheeler 1976), although Marcus (1953) suggests that there are four instars in *P. marcosi*. As a consequence, all of the instars were combined into a single group. The first larvae appear about a week after the eggs are laid, first pupae about two weeks later. Callows are found in the nest about 5 or 6 weeks after the eggs were laid and

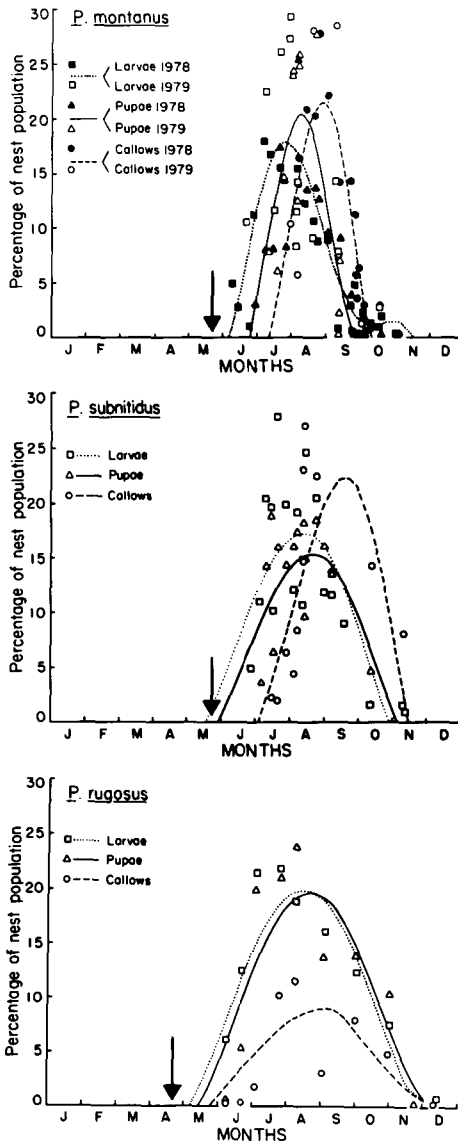


Figure 4. Seasonal changes in the brood populations of three species of *Pogonomyrmex* harvester ants. The arrows indicate the dates when eggs were first found in the nests. Nests excavated which contained only adult workers are not represented in the figure.

remain pale for about three weeks. Thus, development from the egg through the larval instars requires about three weeks, the pupal stage 2–3 weeks, and the callow stage three weeks.

Most of the eggs are laid in the spring as large amounts are found early in the season. The amounts found in later excavations decrease and eggs are rarely found after the pupae begin to appear in the nest.

The larval population reaches a maximum in late July in *P. montanus*, and mid August in *P. subnitidus* and *P. rugosus*. The pupal population reaches a maximum in mid August in *P. montanus* and late August in *P. subnitidus* and *P. rugosus*. The callow population reaches a maximum in early to mid September in all three species. The callows are easy to distinguish from adult workers in *P. montanus* as they remain pale for at least three weeks (based on laboratory observations). The callows of *P. rugosus* and *P. subnitidus* are much more difficult to distinguish from the adult workers. *Pogonomyrmex rugosus* callows darken to a color indistinguishable from mature workers within five days. *Pogonomyrmex subnitidus* mature workers are pale making it difficult to distinguish them from the callows, even if the callows remain pale for many days.

As the majority of the first individuals produced are sexuals, most of the larvae and pupae formed in the first part of the season become reproductives. Workers are also produced early in the season, especially in *P. rugosus*. All of the later brood become workers as was also found in *P. owyheeii* (Willard and Crowell 1965). The reproductives remain in the nest only until late August or early September. In *P. owyheeii* they remain in the nests until mid December (Willard and Crowell 1965).

The first winged reproductives appear in the nests in late June (*P. rugosus*) or late July (*P. montanus* and *P. subnitidus*). The mating flights are completed by the first part of September. The highest sexual populations occur in mid August. Therefore the colony begins production of reproductives early in the year and allows them to remain in the nest for extensive periods of time, even though they are consuming food. This is true to a lesser extent in *P. subnitidus*, where the reproductives appear in the nest in late July and most have left the nest by mid August (Figure 5).

There are several interesting points in Figs. 4 & 5. Although *P. rugosus* begins production earlier in the year than do the other two species, the populations of brood in the nest reach peaks later in the

year. *Pogonomyrmex rugosus* spreads reproduction out over the year to a greater extent than does *P. montanus*. *Pogonomyrmex montanus* produces relatively more sexuals than does *P. rugosus* or *P. subnitidus* and in general the production is much higher.

Mating flights.

The mating flights occur either in the morning (*P. subnitidus*) or the afternoon (*P. montanus* and *P. rugosus*). Reproductives of *P. montanus* first appeared on the nest surface on 10 August 1978. The reproductives emerged from the nest entrance, scurried over the mound for a few seconds and then returned to the nest. They may have been evaluating environmental conditions to determine when it was optimal for the mating flight. This behavior was found in all three species. A small flight occurred on 29 August 1978 between 15:30 and 16:20, a second larger flight occurred on 9 September 1978 between 13:20 and 14:10. The nests of *P. montanus* normally have a single entrance-exit hole. During the large flight on 9 September 1978 the nests had $2.7 \pm 0.3SE$ (12) exit holes per nest (range = 2 to 4). These supplemental exit holes allowed the reproductives to exit the nest more rapidly. I did not observe this behavior in the other two species. Reproductives of *P. subnitidus* were seen on the nest surface as early as 23 July 1980. The flights occurred on 6, 7, and 8 August 1980 between 8:00 and 9:30. In *P. rugosus*, reproductives first appeared on the nest surfaces on 1 August 1979. A large mating swarm was observed on 24 October 1979 between 14:00 and 15:00.

During the time the reproductives left the nest, the surfaces of the nests swarmed with workers. Apparently most or all of these workers were foragers as they were lighter in weight than the other ants in the nest (MacKay, unpubl.). The reproductives often had considerable difficulty becoming airborne, especially the females, which usually climbed up plant stems before flying.

Large mating swarms were observed in *P. rugosus* and were similar to those described by Hölldobler (1976b). The males waited on the tops of hills (over 100 m altitude above surrounding terrain) for the females. The males displayed considerable competition for females as was shown by Markl et al. (1977). As a result mating was a frenzied activity in which numerous males competed for single females by biting, pushing, and in general attempting to exclude

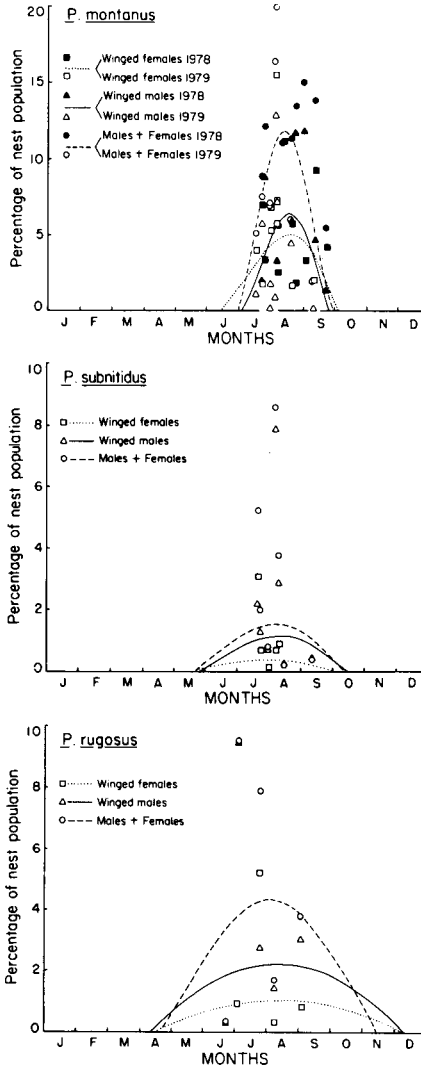


Figure 5. Seasonal changes in the populations of reproductives of three species of *Pogonomyrmex* harvester ants. Note that the percentage scale for reproductives in *P. montanus* has twice the range of the scales for reproductives in the other two species.

other males (See Figure 2 of Hölldobler 1976b and Figure 4 of Markl et al. 1977). Prior to the mating flight, male respiratory rates doubled or tripled (MacKay 1981). The individuals with higher activity levels may be able to increase their fitness by excluding other males from a female or by capturing a female quickly and moving into the copulatory position before other males arrive.

After the female has copulated for a short time, she bites the gaster of the male which is copulating with her. He usually relinquishes his position to another male. There is considerable fighting and tumbling so it is difficult to determine the numbers of times a female mates. Observations suggest that a single female mates at least 3 or 4 times. She may have mated previously with one or more of her brothers in the nest. I observed one mating within the nest of a laboratory colony of *P. montanus*. In all three species, the males attempt to mate with their sisters during emergence from the nest, although a complete copulation was never observed.

After several copulations the females leave the mating swarm either by flying or walking away. The males no longer show interest in such females, as the females apparently stop releasing a pheromone (Hölldobler 1976b). Most females then fly away from the area. A few remain and within a few minutes begin excavating nests near the mating site. As the density of such nests is very high (more than 4 per square meter) the success rate is undoubtedly low. Several times I saw females near the mating area attempt to "steal" the excavation hole of another female, but were chased away by the resident female. Such attempts are common and are occasionally successful (Markl et al. 1977).

Seasonal changes in the positions of inhabitants within the nests.

The seasonal movements in the positions of the inhabitants of the nests depicted in Figures 6, 7 and 8 are similar to those described in *P. owyheeii* (Willard and Crowell 1965) and *P. occidentalis* (Lavigne 1969). The depths are not comparable between the three species as the nests of *P. rugosus* are deeper than those of *P. subnitidus* which are in turn deeper than those of *P. montanus* (Appendix 1). In most cases the time axis is expressed in months of the year with the exception of the sexuals in which only four months are shown. In all cases, the proportions represent means of all nests excavated.

Most of the nest population of *P. montanus*, including the

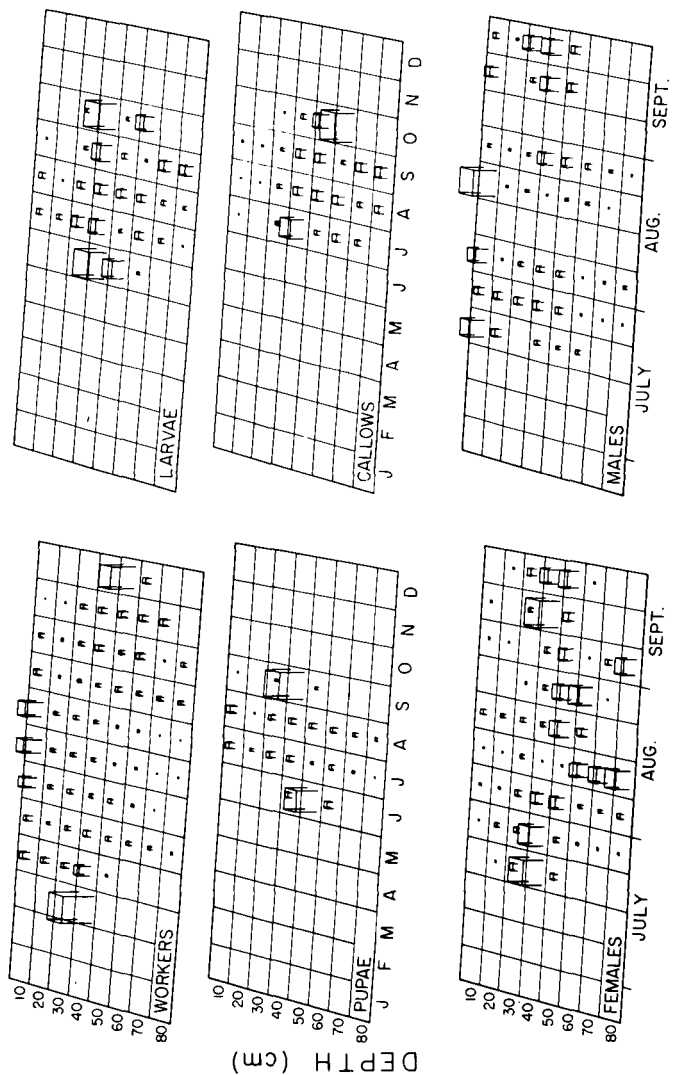


Figure 6. Seasonal movements of the populations of the various member groups in the nests of *P. montanus*. The grid has a value of zero. The value of the proportion of each element in the array is represented both by the height of the box above the grid and the linear dimensions of the box.

workers and the nest queen, overwinter near the 40 cm level of the nest (Figures 6 and 9). In the early spring the soil temperatures are low (Figure 2) and the ants are very sluggish. When the snow begins to melt, the lowest chambers of the nest fill with water. If the ants were at the lowest levels, they would probably be killed. In April and May the *P. montanus* worker population begins to spread throughout the nest. In June, July, and August, nearly 80% of the worker population moves into the upper 10 cm of the nest (Figure 6). During this time the nest temperatures are high and much of the worker population is involved in foraging, brood care, and nest construction. In September as the soil temperature begins to cool, foraging decreases and the workers begin to spread throughout the levels of the nest. In December the workers are again at the 40 or 50 cm level of the nest. The worker population in the 20 and 30 cm levels remains low and relatively constant throughout the year. There is apparently no temporal movement in the larvae or pupae, but they are present within the nest for only part of the year. In general, they are located at the 30 or 40 cm level where temperature and humidity are relatively constant throughout the season. The callows tend to occur in the deeper levels of the nest together with the brood. As most of the worker population is in the upper levels of the nest, the responsibilities of brood care are left to the callows.

It is difficult to make inferences concerning the sexuals as individuals begin to leave the nest in the middle of August. Thus, what appears to be a downward movement may simply be the result of the individuals in the upper levels leaving the nest. The females do tend to occur deeper in the nest than do the males. They may be in lower levels in the nest in order to assist in caring for the brood, as has been observed in the laboratory. It has been shown in *Formica polyctena* that workers must learn brood care during an early period of their lives or they will never care for brood (Jaisson 1975). This could occur in *Pogonomyrmex* where the female reproductives may "learn" brood care so they can later rear their own brood.

The seasonal movement in *P. subnitidus* nests is similar to that found in *P. montanus* nests (Figure 7). A high proportion of the workers remains in the upper 30 cm of the nest. In October there is a dispersion throughout the nest. By December, much of the population is at the 120 to 180 cm level, with little of the population in the lowest parts of the nest. The study area receives less snow than the

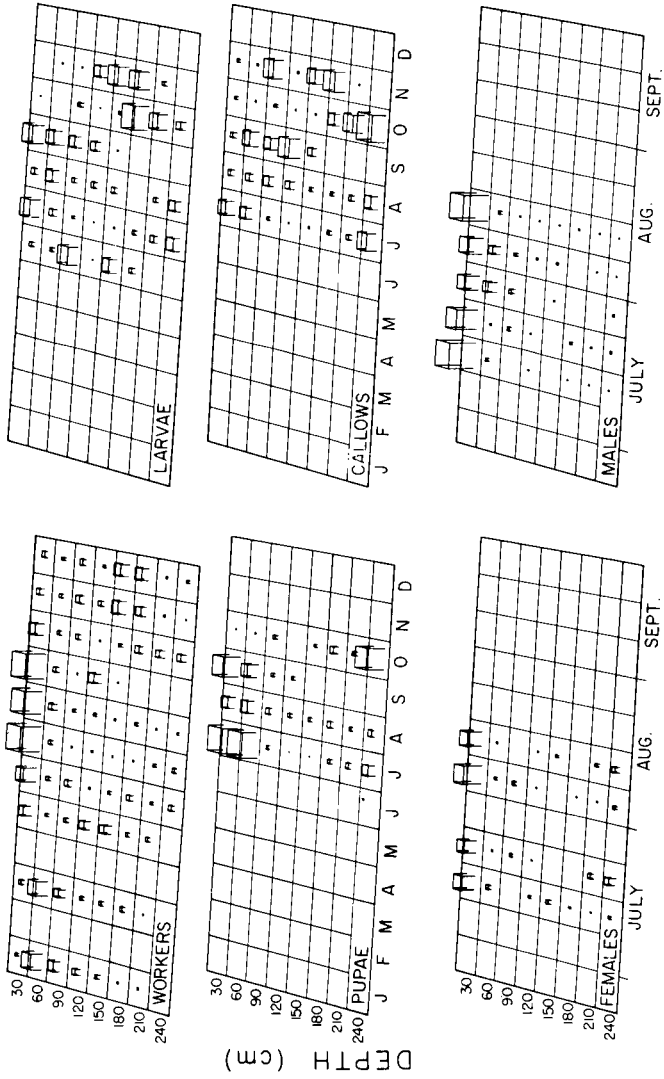


Figure 7. Seasonal movements of the populations of the various member groups in the nests of *P. subnitidus*.

area containing *P. montanus*, but the lower levels of the nest may also become flooded when the snow melts. Many of the larvae and pupae are found in the upper levels of the nest, but there is apparently a downward movement of the brood and callows in October and November. By December there is no brood in the nest. Most of the reproductives are found in the upper 30 cm of the nest (Fig. 7).

The seasonal movements in *P. rugosus* nests are similar to the other two species (Figure 8). Most of the worker population is in the upper levels of the nest throughout the spring and summer. In September and October until December, the ants become distributed throughout the nest. The larvae are dispersed throughout the nest during most of the year, but appear to be moved into the deeper levels of the nest at the beginning of the winter. The pupae are located in the upper levels of the nest but also appear to be moved into the deeper regions of the nest in the fall. The callows also demonstrate a movement into the deeper nest levels in the fall. Again, it is difficult to make inferences concerning the sexuals as they are in the nest for a short period of time, but both sexes appear to be in the upper levels.

In the winter the ants seem to be dispersed throughout the nest and do not avoid the lowest levels of the nest. There is no winter snow at Riverside and the temperatures are higher than those in the mountains (Figure 1), therefore the ants remain somewhat active throughout the year.

The seasonal patterns of distribution within the nests are similar in all three species. The reproductives (when present) and workers are most abundant in the upper levels of the nest, except in the winter. The brood are in the deeper levels where the microclimate undergoes little change. The callows are in the lower levels of the nests in all three species and apparently care for the brood. This is common in ants in general (Wilson 1971) and in *P. badius* (Gentry 1974). No callows were ever seen foraging. They do not quickly darken on exposure to sunlight.

It is commonly stated that ants keep the larvae and pupae separate within the nest to take advantage of the optimal conditions for the development of each (Wheeler 1910; Protomastro 1973). In *Pogonomyrmex*, at least *P. marcus* is reported to practice such behavior (Marcus and Marcus 1951). I have no evidence that the

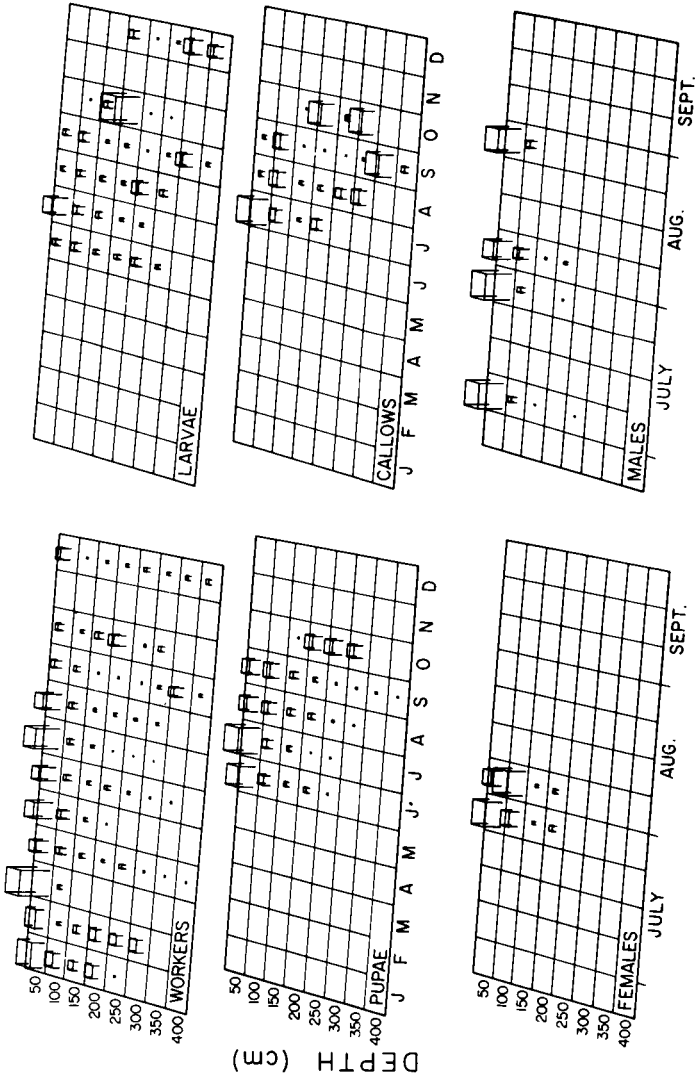


Figure 8. Seasonal movements of the populations of the various member groups in the nests of *P. rugosus*

Table 1. Three-way analysis of variance comparisons of the positions of larvae and pupae in 26 nests of *P. montanus* collected in 1978 and 1979, 3 nests of *P. subnitidus* collected in 1979, and 9 nests of *P. rugosus* collected in 1979. (As the data were expressed as percentages of the total nest population, they were subjected to an arcsin transformation before analysis.)

Source	df	MS	F
<i>P. montanus</i>			
Different nests	25	0.005	0.556 ns
Positions of larvae and pupae	1	0.007	0.778 ns
Levels in nests	7	0.315	35.000***
Nests X brood	25	0.004	0.444 ns
Nests X levels	175	0.110	12.222***
Brood X levels	7	0.028	3.111**
error	174	0.009	
<i>P. subnitidus</i>			
Different nests	2	0.000	0.000 ns
Positions of larvae and pupae	1	0.000	0.000 ns
Levels in nests	22	0.017	5.667***
Nests X brood	2	0.000	0.000 ns
Nests X levels	44	0.017	5.667***
Brood X levels	22	0.003	1.000 ns
error	43	0.003	
<i>P. rugosus</i>			
Different nests	8	0.000	0.000 ns
Positions of larvae and pupae	1	0.000	0.000 ns
Levels in nests	39	0.019	9.500***
Nests X brood	8	0.000	0.000 ns
Nests X levels	312	0.010	5.000***
Brood X levels	39	0.003	1.500 ns
error	311	0.002	

larvae and pupae are placed in separate levels of the nests in any of the three species (Table 1). There is a significant difference between the levels of the nests, which is evident in Figures 6, 7, and 8. The brood tend to be in the lower levels of the nest. Although it is commonly assumed there is segregation of the larvae and pupae, statistical analysis has not been performed in the past to support the assumption.

In one instance, a *P. montanus* nest placed a large number of brood on the soil surface near the nest entrance after a late-summer

Table 2. Analysis of variance comparisons of the positions of males and females in 17 nests of *P. montanus* collected in 1978 and 1979, 4 nests of *P. subnitidus* collected in 1980, and one *P. rugosus* nest collected in 1979. (The data were subjected to an arcsin transformation before analysis.)

Source	df	MS	F
<i>P. montanus</i>			
Different nests	16	0.007	0.538ns
Males and females	1	0.000	0.000ns
Levels in nests	7	0.232	17.846***
Nests X sexuals	16	0.005	0.385ns
Nests X levels	112	0.072	5.538***
Sexuals X levels	7	0.062	4.769***
error	111	0.013	
<i>P. subnitidus</i>			
Different nests	3	0.000	0.044ns
Males and females	1	0.002	0.231ns
Levels in nests	7	0.455	45.083***
Nests X sexuals	3	0.001	0.065ns
Nests X levels	21	0.006	0.630ns
Sexuals X levels	7	0.040	3.924**
error	20	0.010	
<i>P. rugosus</i>			
Males and females	1	0.002	1.000ns
Levels in nest	17	0.006	3.000*
error	16	0.002	

rain, possibly because the upper levels of the nest had become waterlogged. A considerable number of workers guarded the brood during this time and when disturbed, the workers immediately moved the brood back into the nest. This behavior has not been observed in the other two species.

The positions of the males and females were compared with an analysis of variance (Table 2). Although it appears from Figures 6, 7, and 8 and our impressions in the field, that females are in deeper levels of the nest than the males, there is no statistical support (Table 2). There were significant differences between the levels. Figures 6, 7, and 8 illustrate that the reproductives tend to be in the upper levels of the nests.

In *Pogonomyrmex* spp. there is evidence that little mixing of adult workers occurs within the nests (Chew 1960; Golley and

Gentry 1964; Gentry 1974). MacKay (1981) presents data on the respiratory rates and fat contents of workers taken from the different levels of the nests of the three species. In winter, spring, and fall, there are significant differences between the levels with regard to both of these parameters. If mixing of the workers did occur between the different levels of the nest, we would not have found these consistent differences between workers taken from different levels.

There is little evidence of seasonal movements of the nest queens (Figure 9). In the spring *P. occidentalis* queens ascend into the upper levels from the lower levels (Lavigne 1969). The queens may be moved into the deeper regions during the winter for greater protection. In the spring, the soil begins to warm sooner in the superficial levels. The queen may be moved to the higher warmer levels in order to increase her metabolism for initiation of egg production.

Guests.

Many species of insects and spiders were collected within the ant nests. The occurrence of most of these species is probably accidental and individuals of most species were found only in small numbers (one or two individuals per nest). Those species most commonly found include: Orthoptera—*Myrmecophila manni* Schimmer, in the nests of all three species; Coleoptera—*Echinocoleus setiger* Horn, in *P. montanus* and *P. subnitidus* nests, *Hetarius hirsutus* Martin and *H. sp.#1* with *P. montanus*, *H. morsus* Leconte and *H. sp.#2* with *P. subnitidus*, *Cremastocheilus westwoodi* Horn in the nests of *P. subnitidus*. There are at least two species of unidentified staphylinids that are common in *P. subnitidus* nests (more than 10 per nest). Hymenoptera—*Solenopsis molesta* (Say) is common in *P. montanus* and *P. subnitidus* nests, *Pheidole* spp. in *P. rugosus* nests. Of the three harvester ant species, *P. subnitidus* has the greatest number of guests and diversity of species.

Food input into nests.

All three species demonstrate similar seasonal changes in their foraging patterns, with much activity in mid-summer and no activity in the winter and early spring (Figures 10 and 11). There are important differences between the three species. Foraging in *P. rugosus* begins earlier in the spring and extends later into the fall than in the other two species. *Pogonomyrmex subnitidus* has an

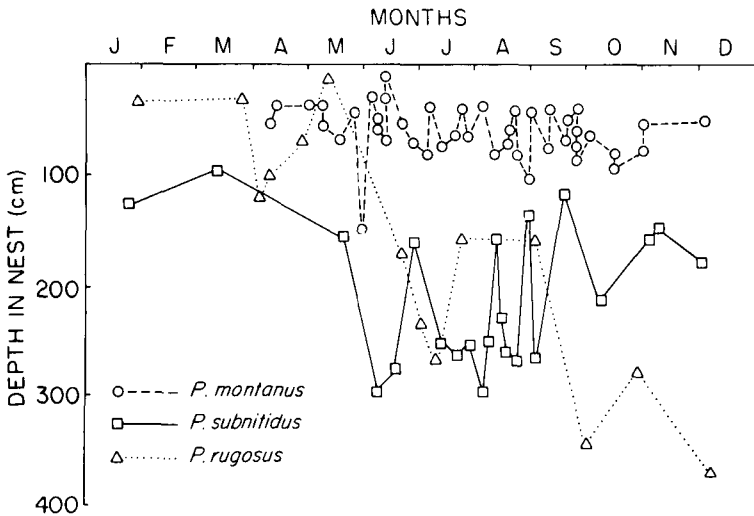


Figure 9. Seasonal changes in the positions of the nest queen in three species of *Pogonomyrmex* harvester ants.

especially short foraging period. *Pogonomyrmex montanus* begins the spring with an abrupt increase in foraging (Figure 10). The lower altitude species, *P. rugosus*, is exposed to many sunny days during the winter. During most of this time the nests of the high altitude species, *P. montanus*, are covered with snow. The nests of the mid altitude species, *P. subnitidus*, are covered by snow part of the time. In May or June foraging begins, increases throughout the summer and decreases again in the fall. This foraging pattern corresponds well with the production of workers and reproductives within the nest.

Only a small portion of the population is involved in foraging. The mean number of foragers per day (recorded during July and August, the months of peak foraging) were 378 ± 73.2 (6) for *P. montanus*, 648 ± 177.3 (4) for *P. subnitidus*, and 1427 ± 187.3 (5) for *P. rugosus*. Later excavation of the nests indicated that the population of foragers comprised 22.9%, 19.4%, and 18.4% of the total nest populations of *P. montanus*, *P. subnitidus*, and *P. rugosus*, respectively. Others have estimated that 10% of the population is involved in foraging in such species as *P. badius* (Golley and Gentry 1964), *P. californicus* (Erickson 1972) and *P.*

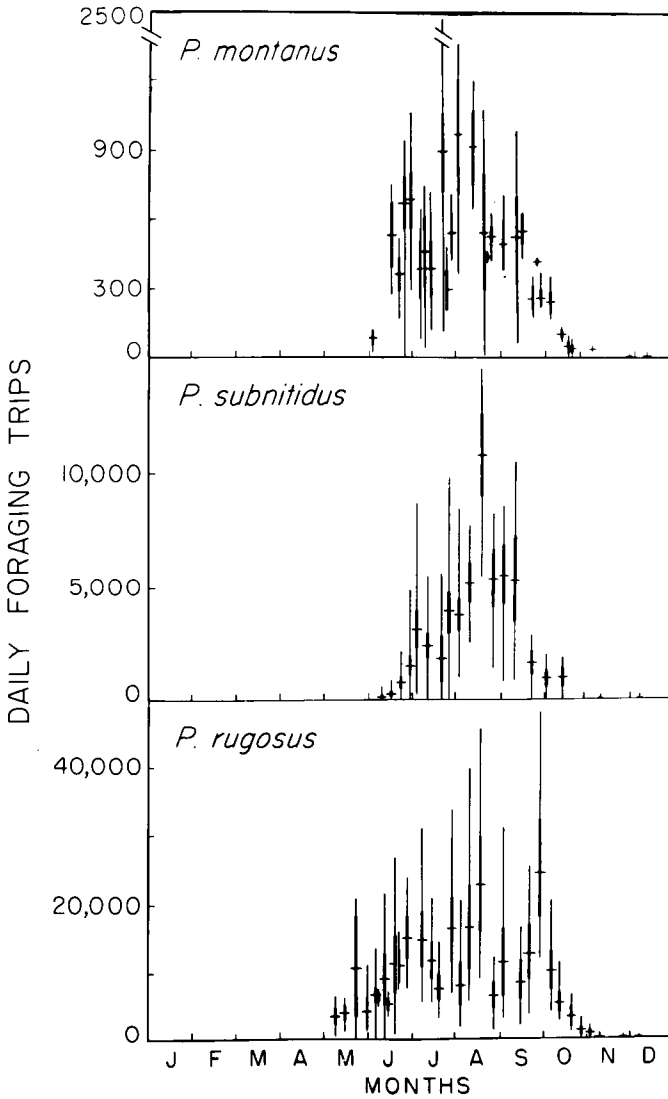


Figure 10. A comparison of the number of daily foraging trips in three species of *Pogonomyrmex* harvester ants. The horizontal lines indicate the means, the black rectangles the standard errors on each side of the mean, and the vertical lines indicate the ranges.

Table 3. Nest densities, populations and biomasses of several ant species of the genus *Pogonomyrmex*. The values are ± 1 standard error, n is presented in parenthesis.

Species	Nests/ha	# adult workers/ nest	# adult workers/ m.sq.	mg d.w. workers/ m.sq.	Locality	Authority
NORTH AMERICAN SPECIES						
<i>apache</i>		40-80			New Mexico	Cole 1954
<i>badius</i>	12-27	4000-6000(6)	13.5	84**	South Carolina	Golley and Gentry 1964
<i>badius</i>		4736 \pm 234 (25) range = 2795-7264			South Carolina	Gentry and Stiritz 1972
<i>barbatus</i> (or <i>rugosus</i> ?)	82	12,358 10,000			Arizona	Wildermuth and Davis 1931
<i>californicus</i>	4-6	1932(1)	1*	1.4*	New Mexico	Whitford 1972
<i>californicus</i>	5.4	4536 \pm 120* (11)	2.4*	3.4*	Southern California	Erickson 1972
<i>desertorum</i>	115	400-600			New Mexico	Whitford and Bryant 1979
<i>magnacanthus</i>		100-225			Southern California	Cole 1968

Table 3 continued

Species	Nests/ha	# adult workers/ nest	# adult workers/ m.sq.	mg d.w. workers/ m.sq.	Locality	Authority
<i>montanus</i>	3-26	1665±88 (70) range= 369-3641	0.5-4.3	1.2-10.1	Southern California	MacKay Unpublished
<i>occidentalis</i>		8700(1)			Arizona	Chew 1960
<i>occidentalis</i>		3024±424 (33)			Wyoming	Lavigne 1969
<i>occidentalis</i>	3-31	2676±348* (11)	0.8-8.3*	25*	Colorado	Rogers et al. 1972
<i>rugosus</i>	21	1000- 3000			New Mexico	Whitford' and Eittershank 1975
<i>rugosus</i>	6.3-20.5	1895±300* (2)	1.2-3.9*	8.6-27.9*	New Mexico	Whitford et al. 1976
<i>rugosus</i>		22,000+			Arizona	Peck 1976
<i>rugosus</i>	1-25	7740±795 (20) range= 2586-14742	0.8-19.4	5.5-137.4	Southern California	MacKay Unpublished
<i>subdentatus</i>		several hundred			Northern California	Cole 1968
<i>subnitidus</i>	1-9	5934±502 (26) range= 1850-13056	0.6-5.3	1.7-15.6	Southern California	MacKay Unpublished

SOUTH AMERICAN SPECIES

<i>brevibarbis</i>	more than 500	Argentina	Kusnezov 1951
<i>carbonarius</i>	400-500	Argentina	Kusnezov 1951
<i>cunicularius</i>	few hundred	Argentina	Bruch 1916, Kusnezov 1951
<i>laticeps</i>	40-50	Argentina	Kusnezov 1951
<i>longibarbis</i>	200-300	Argentina	Kusnezov 1951
<i>marcusi</i>	450 (2)	Bolivia	Marcus and Marcus 1951
<i>mayri</i>	603±79 (8)	Colombia	Kugler, pers. comm.
<i>micans</i>	less than 300 (6)	Argentina	Bruch 1916
<i>rastratus</i>	400-500 or more	Argentina	Kusnezov 1951
<i>uruguayensis</i>	few tens	Argentina	Kusnezov 1951
<i>variabilis</i>	400-500 or more	Argentina	Kusnezov 1951
<i>vermiculatus</i>	400-500 or more	Argentina	Kusnezov 1951

* Estimations based on data from literature.

** From Brian (1965)

occidentalis (Rogers et al. 1972). Chew (1960) estimated that no more than $\frac{1}{2}$ of *P. occidentalis* workers were out of the nest at any one time. In a mark recapture analysis, Whitford et al. (1976) estimated the forager population at 2786 in *P. rugosus*. This estimate is higher than the one I determined which may indicate that the nest populations of *P. rugosus* in New Mexico are larger than those in southern California. My estimates are minimal: there may have been foragers which remained within the nest. Also the experimental channeling of the forager population may have affected the natural foraging activity. The whole work force may not have been activated because of a reduction of recruitment (Hölldobler, Pers. Comm.).

A comparison of the number of foragers given above and the number of foraging trips per day (Figure 10) indicates that individual *P. montanus* foragers make two or three trips per day, *P. subnitidus* foragers about nine, and *P. rugosus* foragers make more than ten trips per day. There are considerable differences between the three species in the numbers of foraging trips made (Figure 10), which compares with the differences in the sizes of the nest populations (Table 3).

The seasonal changes in the daily amount of food brought to the nest are similar to those found in the numbers of foraging trips (Figure 11). As with the forager number, *P. rugosus* brings in food earlier in the spring and extends foraging later into the fall, compared to the other two species. *Pogonomyrmex montanus* abruptly increases the food input once foraging begins and decreases it slowly until fall. *Pogonomyrmex montanus* is the only species of the three which does not store seeds in the nests. It may have to bring in large amounts of food once the larvae begin to appear in the nest. The other two species have seed reserves and may thus avoid such an abrupt increase in foraging in the spring.

Comparisons of the food sources of the three species (Figure 12) indicate that the harvester ants utilize a wide variety of food items, although most materials are either seeds or plant parts. *Pogonomyrmex rugosus* relies almost exclusively on seeds. *Pogonomyrmex subnitidus* and especially *P. montanus* bring a much greater diversity of food items to the nest. *Pogonomyrmex montanus* relies more heavily on plant parts and insects than does *P. subnitidus*. *Pogonomyrmex subnitidus* brings in a greater proportion of feces than does *P. montanus*, although the ratio of bird to mammal feces

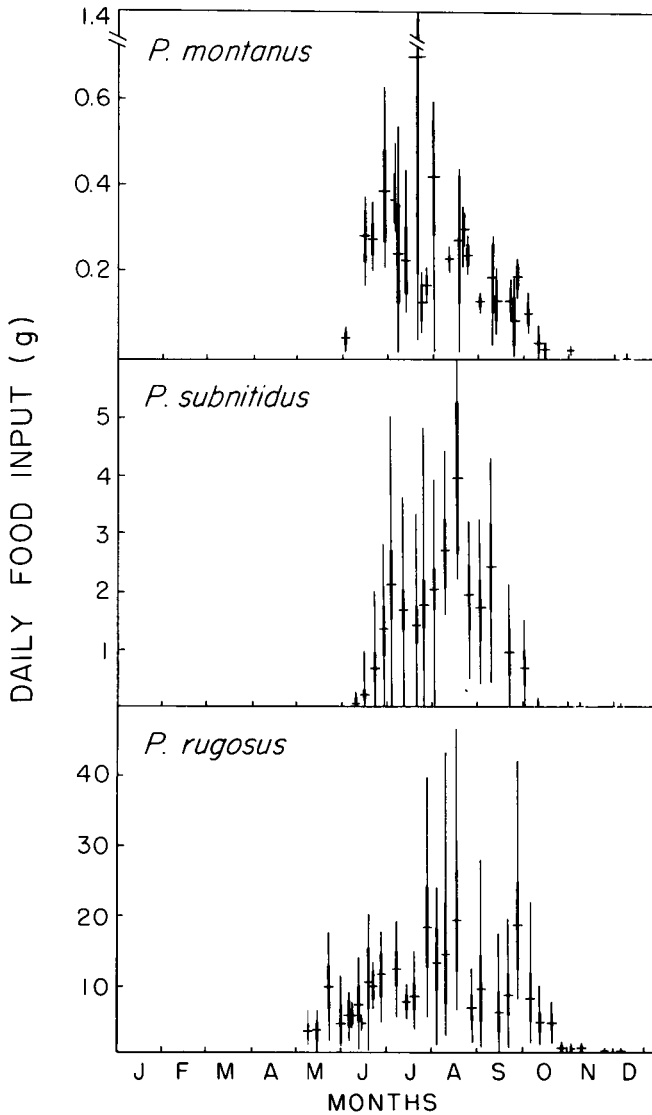


Figure 11. A comparison of the daily food input (grams) in the three species of *Pogonomyrmex* harvester ants.

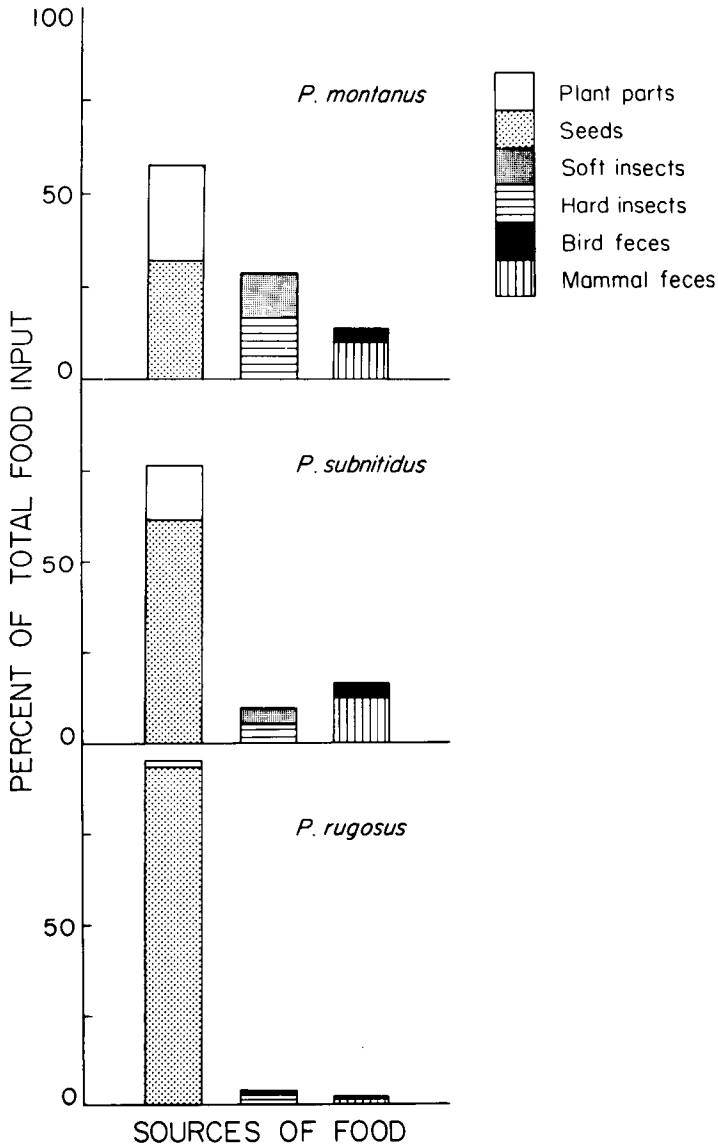


Figure 12. A comparison of the food sources in the three species of *Pogonomyrmex* harvester ants.

is similar in both species. *Pogonomyrmex rugosus* brings in more bird feces than mammal feces, *P. montanus* and *P. subnitidus* bring in more mammal feces than bird feces. A distinction was made between "hard" insects and "soft" insects. Hard insects included those heavily chitinized forms, especially the Coleoptera and certain Formicidae. Soft insects included Homoptera, most Hemiptera, most Diptera, larvae and pupae of most orders and a few non-insects such as spiders. It appears that the degree of chitinization may not be important as the proportions of hard and soft insects were similar. All three species have chitinase activity in their gasters (MacKay, unpub. data).

Plant parts consist of pieces of leaves and flowers and in the case of *P. montanus*, pine resin. Flowers of *Penstemon* spp. and *Arctostaphylos* spp. are transported to the nest and placed around the brood, possibly to increase the humidity. Later the intact flowers are discarded at the nest surface. This indicates the flowers are not placed around the brood to protect them from predators. In the case of pieces of leaves, apparently they are eaten by the ants as they do not later appear on the nest surface. There is considerable seasonal change in the food composition of *P. montanus* and *P. subnitidus* (Figure 13). The percentages of insects brought into *P. montanus* nests changes little seasonally. There is a seasonal reduction in the percentage of utilization of insects in *P. subnitidus*. There is little seasonal change in the proportion of the food sources composed of feces in the two species, although a slight reduction may occur. In both species, especially *P. montanus*, there is a seasonal decrease in the proportion of plant parts brought to the nest. In both species, there is a dramatic increase in the utilization of seeds after July. This increase is probably related to a greater availability of seeds after the flowering period of annual plants. A similar comparison was not made in the case of *P. rugosus* as non-seed materials are a very small portion of their diet (Fig. 12). In *P. rugosus*, there was a seasonal drop in the proportion of the diet composed of *Erodium cicutarium* (L.) L'Her. seeds (May 90.3%, June 91.0%, July 88.9%, August 89.7%, September 84.1%, and October 80.9%). Other seeds, especially those of *Pectocarya linearis* DC and *Festuca octoflora* Walt., made up most of the difference.

Caloric analysis of the food entering the nests of the three species indicates that a *P. montanus* colony receives an average of 166.6

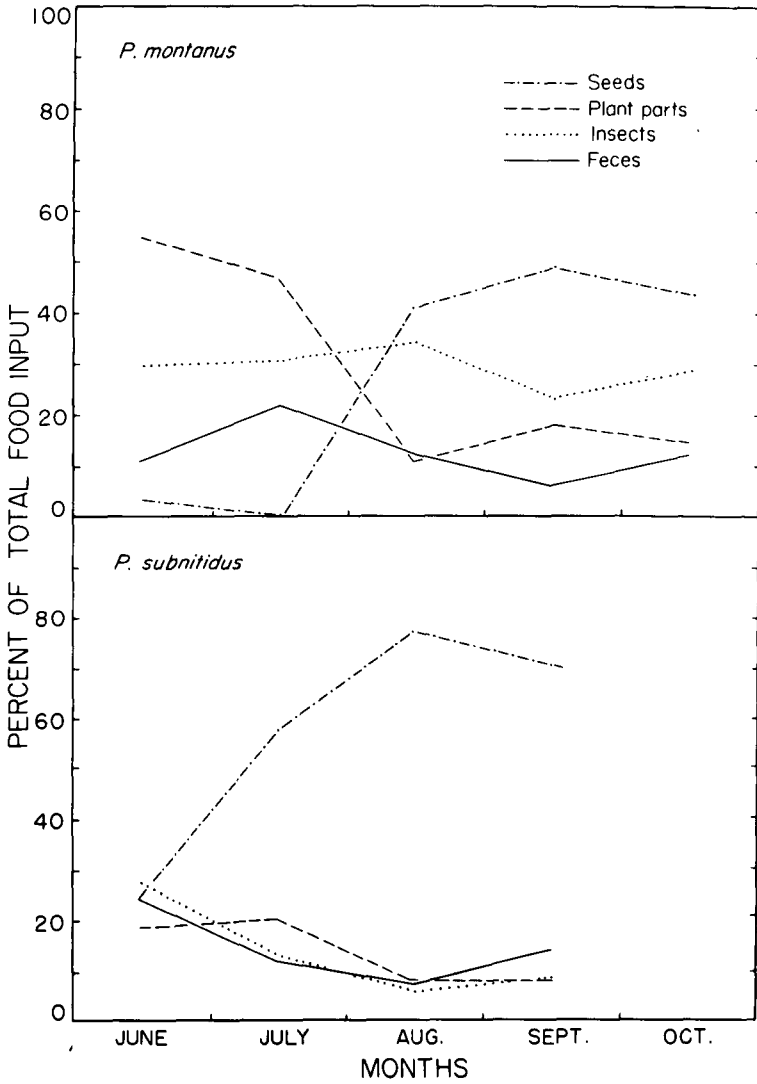


Figure 13. The seasonal changes in the food sources of *P. montanus* and *P. subnitidus*.

kcal, a *P. subnitidus* nest 1267.0 kcal, and a *P. rugosus* nest 7613.6 kcal of food during a year (MacKay 1981). Of these amounts, a *P. rugosus* colony discards seed husks and other such materials, a quantity consisting of 5004.5 kcal or 65.7% of the intake. This is indicated in the field by large discard piles of seed husks being deposited around the nests. A few seeds are discarded and germinate from the piles in the spring. Another harvester ant, *Veromessor pergandei* (Mayr) forages in the piles and removes many of the discarded seeds. *Pogonomyrmex montanus* and *P. subnitidus* discard few materials, the amounts are too small to be estimated.

Seed storage.

Seasonal changes in seed storage in *P. subnitidus* and *P. rugosus* are shown on Figure 14. *Pogonomyrmex rugosus* began both 1979 and 1980 (data for January) with 0.04–0.06 grams of seed storage per ant. The correlation of ant number vs. seed weight was very high ($r = 0.997$, $p < 0.01$). This amount dropped until May, possibly the

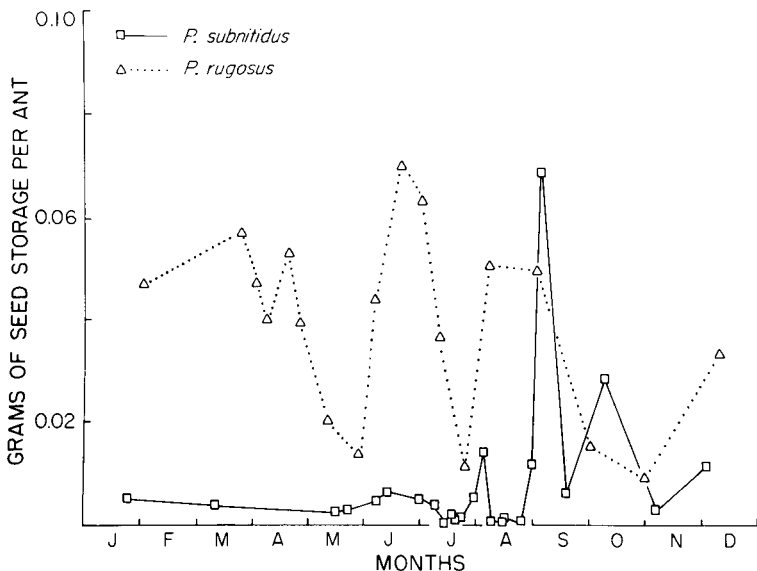


Figure 14. A comparison of the seasonal changes of seed storage in *P. rugosus* and *P. subnitidus*.

result of seed consumption by the developing larvae. I have no explanation for the other two peaks which appear. There is some evidence of a drop in seed storage in the spring in *P. subnitidus*, but it is not as great as that found in *P. rugosus*. *Pogonomyrmex subnitidus* also appears to begin the season with a constant amount of seeds, about 0.002–0.004 g/ant, much smaller quantities than *P. rugosus*. There are also many unexplained peaks in *P. subnitidus* seed storage, especially the high peak in September. *Pogonomyrmex montanus* does not store seeds in the nest. In the population at Big Pine Flats in the San Bernardino Mountains, we occasionally encountered very small caches of seeds (less than 0.0001 g/ant) which were apparently only small daily accumulations of seeds that had not been eaten at that time.

Production.

Production in the three species is summarized in Table 4. The proportion of energy invested in production varies considerably between the three species, but in all cases it is relatively low. Total production constitutes 12.2, 8.3, and 7.9 per cent of the total energy flow in *P. montanus*, *P. subnitidus*, and *P. rugosus* respectively (MacKay 1981). In all three species, a higher percentage of the total production is invested in workers than reproductives (Table 4). *Pogonomyrmex subnitidus* and *P. rugosus* both invest heavily in workers, *P. montanus* invests heavily in reproductives. The data on Table 4 suggest that the three species invest more in the production of females than in males. The costs of respiration of males are higher than of females (MacKay 1981). When respiration costs are taken into account, the colonies of each species invest about equally in the production of males and females (MacKay 1981). More numbers of males than females are produced in all three species (Table 4). Individual females are more expensive to produce than are individual males (MacKay 1981).

Most of the workers are replaced each year. *Pogonomyrmex montanus* colonies produce 1516 workers per year (Table 4), which is similar to the mean worker population of 1665 (Table 3). *Pogonomyrmex subnitidus* colonies produce 3988 workers as compared to a worker nest population of 5934; *P. rugosus* colonies produce 5298 workers per year compared to a worker nest population of 7740.

Table 4. A comparison of the investments in production in three species of *Pogonomyrmex* harvester ants.

Species	Group	Number of Individuals	Dry wt (g)	kcal	Percent Total Production
<i>montanus</i>	Workers	1516± 95	2.4	12.7	51.8
	Females	187± 30	1.2	7.8	31.8
	Males	239± 41	0.8	4.0	16.3
				24.5	
<i>subnitidus</i>	Workers	3988±438	11.6	87.4	91.5
	Females	111± 65	0.9	5.4	5.7
	Males	251± 87	0.6	2.7	2.8
				95.5	
<i>rugosus</i>	Workers	5298±763	30.3	208.2	86.6
	Females	118±100	2.7	18.9	7.9
	Males	312± 73	2.5	13.4	5.6
				240.5	

DISCUSSION

Comparison with other species in the genus *Pogonomyrmex*.

The genus *Pogonomyrmex* belongs to the tribe Myrmicini, one of the most primitive tribes in the subfamily Myrmicinae. The genus has existed at least since the Oligocene (Burnham 1978), and is distributed throughout North and South America from Canada to Patagonia, from sea level to at least 4500 meters in altitude. At the present time there are 24 valid species in North America and about 33 in Central and South America. The genus may have originated in South America and migrated northward (Kusnezov 1951) or originated in North America and migrated southward (Wheeler 1914; Creighton 1952).

Considerable work has been done on nest densities, populations, and biomasses of ants of various species of the genus *Pogonomyrmex* (Table 3). Examples of biomasses from other genera would include the following (expressed as mg dry weight/m²), *Tetramorium caespitum* at 200 (Brian et al. 1967) and 1480 (Nielsen 1974), *Lasius niger* at 60 (Odum and Pontin 1961) and 1060 (Nielsen 1974), *L. alienus* at 2090 (Nielsen 1974), *L. flavus* at 1400 (Odum and Pontin 1961) and 15,000 (Waloff and Blackith 1962), *Leptothorax acervorum* at 3000 (Brian 1956), and *Formica rufa* at 12,000

(Marikovskiy 1962). In general, the biomasses of *Pogonomyrmex* are much lower than those found in other genera.

The species investigated, especially *P. subnitidus* and *P. rugosus*, are comparable to most of the North American representatives of the genus (Table 3). The South American species apparently have much smaller populations, but few nests have been excavated and most were partial excavations in which the queen was not found or after the excavation was finished, additional ants were found later. Species from arid regions tend to have larger colonies than those from mesic environments, with the exception of *P. laticeps*. The colonies of North American species live longer than South American species (Kusnezov 1951). *Pogonomyrmex montanus* is somewhat atypical for the genus in occurring at higher altitudes, but is similar to other species in several aspects. The number of nests per hectare is comparable to several other species including *P. badius*, *P. barbatus*, *P. occidentalis*, *P. owyheeii*, *P. rugosus*, and *P. subnitidus*. The nest populations of *P. montanus* are smaller than those of most of the other species, but the number of workers/m.sq. and/or the dry wt/m.sq. are comparable to *P. badius*, *P. californicus*, *P. occidentalis*, *P. owyheeii*, *P. rugosus*, and *P. subnitidus*.

With regards to the populations, the three species investigated appear to be "typical" North American *Pogonomyrmex* harvester ants. It would be very interesting to do a comparable study of "typical" South American *Pogonomyrmex* harvester ants.

Effect of altitude.

It was anticipated that altitude would have three primary effects: 1) The higher altitude species, *P. montanus*, would be subjected to lower average temperatures. 2) The higher altitude species would be subjected to shorter foraging seasons, thus reducing the yearly food input into the nest, resulting in lower production. 3. The higher altitude's shorter growing season would result in fewer available seeds from annual plants.

Although *P. montanus* is subjected to the lowest seasonal temperatures of the specific populations of the three species investigated (Figure 2), it metabolically compensates for this by having higher respiratory rates than the other species (MacKay 1981). Apparently altitude has an effect on foraging, although it was not as large as expected. The foraging season was somewhat reduced in *P. montanus* and *P. subnitidus*, when they are compared

with *P. rugosus* (Figure 10). *Pogonomyrmex montanus*, and to some extent *P. subnitidus*, are in habitats with winter snow cover. In such habitats foraging during the winter is not possible. *Pogonomyrmex rugosus* occupies a low altitude habitat where there are many warm sunny days during the winter. During these days, it does not forage, although a few workers are on the nest surface either sunning themselves or working on nest reconstruction.

The higher altitudes had shorter growing seasons, resulting in fewer annual seed producing plants. As a result *P. montanus* and *P. subnitidus* foraged on various materials but began to rely heavily on seeds later in the year (Figure 13). This was especially the case in *P. montanus*, which relied heavily on plant parts early in the year. Later when seeds became more available, they almost completely replaced plant parts in the diet (Figure 13).

Allocation of resources between worker and reproductive production.

As was expected, the highest altitude species was exposed to a shorter foraging season, but this did not result in lower production. The highest altitude species, *P. montanus*, invests a larger proportion of energy into production than do the other two species. The amount invested in reproductives is especially high (Table 4). *Pogonomyrmex subnitidus* and *P. rugosus* invested about equally in production, with investment in reproductives very low compared to *P. montanus* (Table 4).

Most *Pogonomyrmex* spp. are low altitude desert species (Cole 1968). *Pogonomyrmex montanus* appears to be in a marginal habitat for *Pogonomyrmex* spp. in that it occurs in a high altitude pine forest. The nest populations are among the smallest for the genus (Table 3) and the nests are also very shallow (Appendix 1). Both *P. montanus* and *P. subnitidus* have shorter foraging seasons and apparently are not able to exploit their optimal food source (seeds) until late in the season (Figure 13). Simulations of the effects of bad years on the nests indicate that *P. rugosus* and *P. subnitidus* are able to withstand moderately large reductions in food input whereas *P. montanus* is not (MacKay in prep.). As a result, nests may be short-lived as compared to the other two species and nest-extinction may be a common phenomenon. Apparently, as a response to such conditions, *P. montanus* invests a larger proportion of energy in the production of reproductives than do the other

two species. It might be expected that the South American species would be ecologically similar to *P. montanus* as they share many characteristics (Table 3).

Production as well as foraging and food input were spread over more of the season in *P. rugosus* than in the other two species (Figs. 4, 5, 10 & 11). This is easily explained as *P. rugosus* lives in a more moderate climate than the other two species. Actually it was expected that these processes would occur over the entire year as there are many warm sunny days at lower elevations during the winter. Yet, activities almost stop. Perhaps these processes do not continue as the nest temperatures are lower during the winter than they are in the summer (Figure 2).

The sex ratio was not constant between years (see data in Appendix 1). In *P. montanus* the female:male ratio was 0.88:1 in 1978, 1.41:1 in 1979, and 0.42:1 in 1980. In 1980 the number of males produced was three times those of the other years. An excess of females in 1979 was not found in *P. rugosus* (0.38:1) as was found in *P. montanus*. An excess of males was found in *P. subnitidus* (0.42:1) in 1980 as was found in *P. montanus*.

Nests are extremely heterogeneous in regards to sex ratio (Appendix 1). Correlations were investigated between the female:male ratio and the apparent age of the nest. Twelve *P. montanus* nests at the peak levels of production were used in the analysis. The age of a nest should be related to the numbers of adult workers present in the nest and the depth of the nest: older nests should be deeper and have a larger worker population. The product-moment correlation coefficients (Sokal and Rohlf 1969) of the sex ratio with worker population size and nest depths were both 0.17. Although the coefficients were not statistically significant, both were positive, suggesting that older nests produced greater proportions of females. The product-moment correlation coefficient comparing the sex ratio with the numbers of workers produced by the nest during the year was negative ($r = -0.38$). Although the relationship was not statistically significant, it suggested that nests involved in an increase in the worker population (i.e., younger nests) produced a smaller proportion of females. Data were presented (MacKay 1981) which indicated that food stressed nests produced a greater proportion of females; nests given extra food produced a greater proportion of males.

The factors influencing the determination of sex ratios in the Hymenoptera are currently of much interest (Herbers 1979). Experimental manipulation of food input and excavation of colonies of known age may provide information on the factors which determine the sex ratio in a harvester ant nest.

SUMMARY

This investigation compares the phenologies of foraging and reproduction in three species of *Pogonomyrmex* harvester ants along an altitudinal transect in southern California, USA. Periodic excavations of 126 nests of the three species, *P. montanus*, *P. subnitidus*, and *P. rugosus*, reveal that seasonal changes occur within the nests. The three species have similarities in the physical environment of the nest although *P. montanus*, the highest altitude species, has lower nest temperatures. Both *P. montanus* and *P. subnitidus* are snowbound during part of the season. Egg laying begins in late April or May; development to adult requires five to six weeks. The brood reach maximum numbers in late July to late August. Most of the larvae and pupae formed in the first part of the season become reproductives. Mating flights begin in late July and are completed by the first part of September. The highest reproductive populations occur in mid August.

Much of the nest population is in the upper levels of the nest during the summer and in the lower levels during the winter. During the summer, temperature and humidity gradients exist in the nests with deeper levels being cooler and moister. These gradients may account for the placement of the brood in the lower levels. There is no evidence of segregation of the larvae and pupae within the nest, which has been reported by other investigators.

All three species demonstrate similar seasonal changes in foraging patterns, with much activity in the mid summer and no activity during the winter. Only about 20% of the nest population is involved in foraging. Individual foragers make up to 9 or more foraging trips per day. The ants utilize a wide variety of food items, although most materials are either seeds or plant parts. There is a considerable seasonal change in the food composition of *P. montanus* and *P. subnitidus*.

The highest altitude species, *P. montanus*, allocates more energy to reproduction than do the mid or low altitude species. The nests

invest about equally in the production of males and females. Evidence presented suggests that the sex ratio may be ecologically determined and that there may be a yearly change in the sex ratio.

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Appendix 1. List of the populations of the excavated *Pogonomyrmex* spp. nests, including workers (W), larvae (L), pupae (P), callows (C), males (M), and females (F). The position of the queen and maximum depth of the nests are expressed in centimeters. The dates indicated are when the excavation was begun.

Date	W	L	P	C	F	M	Position of queen	Depth
<i>Pogonomyrmex montanus</i>								
21 Sept 77	793	7	514	0	0	0	50	50
23 Sept 77	1918	123	578	0	0	0	40	40

Appendix 1. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
11 Apr 78	3142	0	0	0	0	0	50	50
13 Apr 78	1654	0	0	0	0	0	40	50
16 Apr 78	1874	0	0	0	0	0	*	40
3 May 78	2372	0	0	0	0	0	38	70
8 May 78	2240	0	0	0	0	0	36	60
9 May 78	3641	0	0	0	0	0	55	70
18 May 78	2277	0	0	0	0	0	65	80
25 May 78	1752	0	0	0	0	0	43	60
31 May 78	1951	0	0	0	0	0	75	75
6 June 78	491	0	0	0	0	0	32	50
8 June 78	1598	83	0	0	0	0	47	59
13 June 78	499	0	0	0	0	0	*	30
13 June 78	1841	51	0	0	0	0	10	65
23 June 78	695	7	0	0	0	0	55	60
27 June 78	1087	141	38	0	0	0	*	70
7 July 78	1488	359	160	0	0	0	39	80
12 July 78	1652	367	177	0	0	0	75	75
20 July 78	1604	426	477	0	188	54	68	68
24 July 78	1033	228	131	0	52	138	40	70
4 Aug 78	996	411	678	438	64	87	39	53
11 Aug 78	1013	290	323	496	262	0	80	82
18 Aug 78	1158	277	358	529	147	148	60	70
22 Aug 78	1057	244	359	784	48	327	40	82
30 Aug 78	1552	306	330	766	111	405	40	105
9 Sept 78	1113	14	163	254	162	83	40	75
19 Sept 78	1443	54	73	281	81	25	50	68
23 Sept 78	631	1	0	80	0	0	40	63
23 Sept 78	2271	10	2	128	1	0	70	83
24 Sept 78	2573	4	6	96	0	1	60	73
26 Sept 78	634	0	0	40	0	1	*	110
26 Sept 78	1734	5	3	117	0	0	*	84
30 Sept 78	1785	24	12	52	0	0	60	64
30 Sept 78	1024	0	0	13	0	0	59	59
30 Sept 78	652	15	1	11	0	0	**	86
7 Oct 78	1245	16	0	11	0	0	*	74
14 Oct 78	2105	20	3	63	0	0	80	92
16 Oct 78	1343	24	0	0	0	0	**	43
16 Oct 78	538	49	0	0	0	0	**	40
27 Oct 78	2812	4	0	4	1	0	50	76
7 May 79	1304	0	0	0	0	0	30	53
7 May 79	3585	0	0	0	0	0	*	61
25 May 79	2194	0	0	0	0	0	50	70
25 May 79	3141	0	0	0	0	0	40	80

Appendix I. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
3 June 79	1605	0	0	0	0	0	**	40
15 June 79	1979	0	0	0	0	0	30	70
20 June 79	537	63	0	0	0	0	*	50
20 June 79	1768	0	0	0	0	0	20	60
8 July 79	599	193	67	0	0	0	50	60
16 July 79	563	84	44	0	28	8	50	50
22 July 79	2614	1318	750	0	86	290	50	60
29 July 79	947	813	710	305	198	2	40	50
29 July 79	1777	383	708	7	286	146	70	80
30 July 79	369	27	21	137	15	2	*	80
30 July 79	1111	835	693	13	149	51	60	60
3 Aug 79	1853	325	490	609	601	37	*	120
4 Aug 79	1261	483	1049	595	305	543	*	100
4 Aug 79	1625	555	1013	225	221	277	60	80
12 Aug 79 (a)	976	345	534	752	167	12	50	60
12 Aug 79 (b)	640	124	231	701	144	0	30	80
13 Aug 79 (a)	1063	619	529	495	390	11	*	50
13 Aug 79 (b)	697	244	466	660	387	85	40	70
18 Aug 79	755	234	719	729	41	113	60	70
19 Aug 79 (c)	370	4	0	107	221	4	50	70
19 Aug 79 (c)	520	108	641	322	72	262	*	50
19 Aug 79 (d)	836	168	632	1068	142	55	80	80
20 Aug 79 (d)	792	81	401	655	141	0	40	80
20 Aug 79 (e)	596	169	0	36	33	318	50	50
20 Aug 79 (e)	1079	574	839	289	54	436	50	60
7 Sept 79	1796	468	5	931	62	1	80	110
8 Sept 79	711	67	19	65	0	0	30	30
8 Sept 79	808	126	112	559	0	0	70	70
14 Oct 79	1308	35	0	0	0	0	60	60
5 Dec 79	1504	0	0	0	0	0	50	70
19 Aug 80	1039	nr	nr	780	216	309	**	nr
20 Aug 80	1388	nr	nr	501	255	343	**	nr
21 Aug 80	1346	nr	nr	144	53	274	**	nr
21 Aug 80	1687	nr	nr	351	39	634	**	nr
22 Aug 80	1800	nr	nr	185	310	516	**	nr
<i>Pogonomyrmex subnitidus</i>								
5 Nov 78	5033	47	0	0	0	0	150	210
29 Aug 79	2507	894	1212	2819	0	0	140	170
15 Sept 79	3612	867	892	4147	0	0	120	150
7 Oct 79	5442	109	321	999	0	0	220	230
3 Nov 79	3452	56	0	315	0	0	160	230
30 Nov 79	5182	0	0	0	0	0	180	240

Appendix 1. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
25 Jan 80	6864	0	0	0	0	0	130	210
12 Mar 80	13056	0	0	0	0	0	100	200
16 May 80	5009	0	0	0	0	0	*	210
22 May 80	7687	0	0	0	0	0	150	150
6 June 80	4962	0	0	0	0	0	300	300
12 June 80	8679	0	0	0	0	0	*	270
30 June 80	10160	531	0	0	0	0	160	180
8 July 80	3515	470	153	0	0	0	*	260
13 July 80	2440	784	541	0	0	0	260	260
17 July 80	1784	609	579	66	0	0	*	140
19 July 80	9385	1238	767	0	368	270	*	280
22 July 80	3619	1977	1139	143	47	94	270	280
29 July 80	5215	1817	1301	570	6	66	260	260
4 Aug 80	4060	850	1127	314	52	554	*	300
7 Aug 80	4734	1816	1646	794	80	271	190	250
12 Aug 80	2420	559	953	1207	1	8	110	150
13 Aug 80	2362	750	484	1355	0	0	60	230
14 Aug 80	3877	2145	1300	1305	0	0	270	270
23 Aug 80	4168	2301	2062	2524	0	0	250	280
4 Sept 80	6901	1359	1567	1591	2	49	270	270

Pogonomyrmex rugosus

19 Nov 78	4569	0	0	0	0	0	110	200
25 Mar 79	3707	0	0	0	0	0	30	130
3 Apr 79	3778	0	0	0	0	0	120	240
8 Apr 79	14742	0	0	0	0	0	100	360
20 Apr 79	3115	0	0	0	0	0	*	270
27 Apr 79	11802	0	0	0	0	0	70	125
11 May 79	7275	0	0	0	0	0	10	160
28 May 79	10588	0	0	0	0	0	30	160
6 June 79	8033	532	37	0	0	0	*	300
20 June 79	9214	1411	594	22	0	0	170	190
2 July 79	2485	1136	1057	101	5	505	240	260
10 July 79	9374	1522	1368	21	0	0	270	280
24 July 79	3086	1753	1693	838	418	219	160	180
6 Aug 79	5648	2440	3072	1501	38	181	*	300
31 Aug 79	7219	1839	1565	365	9	342	160	270
28 Sept 79	11640	2204	2483	1440	0	0	350	360
27 Oct 79	4655	465	633	305	0	0	280	280
7 Dec 79	10538	66	0	0	0	0	370	400
1 Feb 80	7503	0	0	0	0	0	40	210
23 Feb 80	11239	0	0	0	0	0	*	300

Appendix I. cont.

* Nest queen not found.

** Nest queen found but level not recorded.

(a) Nest received extra food in June 1979.

(b) Nest received extra food in July 1979.

(c) Nest received less food throughout 1979 season.

(d) Control nest.

(e) Nest received extra food throughout 1979 season.

See MacKay (1981) for further details.

nr= not recorded.